5

Biological Factors Influencing Nutrient Supply in Forest Soils

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I. INTRODUCTION

The influence of biological factors on nutrient supply is complex and there are many ways of organizing a discussion of them. I have chosen to categorize the factors by various structural and functional properties on the premise that these would relate more easily to management practices. Pure stands will be discussed primarily; however, they will be contrasted with mixed stands, natural and artificial. Succession also will be addressed to emphasize further the importance of species change on nutrient availability.

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The organization of material into structural and functional properties affecting nutrient availability is intended to reveal how different forests and forest conditions affect the biological processes controlling nutrient availability. Understanding these processes is the key to managing them.

II. DECOMPOSITION PROCESSES

The significance of the decomposition process can be assessed by considering the fate of organic matter (net primary production, NPP) in a forest ecosystem. Twenty to sixty percent of the NPP of immature forest plantations is in perennial tissues (i.e. the stem and branches). A portion of the annual production may be consumed by herbivores, but in most forest systems this is less than 10% (Bray and Gorham, 1964). Occasional outbreaks of insect herbivores may defoliate forests and in those instances greatly influence many ecosystem processes. The major fate of NPP is its transfer to the forest floor and soil as litter, faeces and soluble organic matter. In all mature forests this transfer accounts for the majority of NPP (Gosz *et al.*, 1978); only in very young, fast growing forests does biomass increment exceed litter production. The decomposition of this large amount of litter has two important results: the formation of soil organic matter and the mineralization or release of essential elements. Whether decomposition can degrade organic matter at a rate equal to litter production is a factor of paramount importance in determining nutrient availability.

A. Role of Soil Fauna

The importance of soil animals can best be appreciated by examining their density and diversity. A temperate woodland soil with a well developed litter and humus layer may contain more than a thousand species of soil animals with a total population of several millions m^{-2} in the top 5 cm of the profile (Swift *et al.*, 1979). Decomposition studies suggest that weight and element loss from litter may be increased up to an additional 25% during the first year by the presence of fauna. This is due to a number of factors, but the quality of the litter is of considerable importance. Deciduous tree leaves rank in terms of their palatability to soil animals and remain in approximately the same order irrespective of whether the feeding is carried out with earthworms, millipedes or microarthopods at the class, family, genus or species level (Swift *et al.*, 1979). However, there are major differences in the soil organism communities of different biomes (Table I). The amount of organic

Table I. Soil fauna and microflora populations in major ecosystem types.[a]

		Boreal forest (mor soil)	Warm temperate forest (mull soil)	Tropical savannah	Tropical forest
		no. m^{-2}			
Microfauna	Nematoda	270×10^6	200×10^6	30 000	65 000
	Protozoa				
Mesofauna	Collembola	400 000	40 000	2000	15 000
	Acari				
	Enchytraeidae	750 000	30 000	0–400	0–1000
	Isoptera	0	0	4000	5000
	Diplura	1000	500	500	1000
	Symphyla				
	Protura				
	Diptera				
	Total	1 151 000	71 500	6900	22 000
Macrofauna	Earthworms	20	200	1–100	0–250
	Diplopoda	500	1000	< 1	400
	Isopoda				
	Coleoptera	300	200	100	1000
	Mollusca				
	Orthoptera				
	Dermaptera				
	Total	820	1400	200	1650
		(no. g^{-1} soil)			
Microflora	Bacteria	5×10^6	6×10^6	55×10^6	50×10^6
		(m hyphae g^{-1} soil)			
	Fungi	4000	3000		6000

[a] From Swift *et al.* (1979).

matter in the soil, and the climatic conditions which influence the accumulation of organic material influence microfauna and mesofauna population sizes. For example, the Nematoda and Protozoa inhabit water films which are influenced markedly by organic matter, and the hot, dry mineral soils of the tropics have low populations of these two orders. The deep organic soils of the temperate forests maintain the highest populations of mesofauna (Collembola, Acari and Enchytraeidae). Deciduous and conifer tree vegetation producing acid litter (mor) decrease earthworms, millipedes and, to some extent, Isopoda and increase Protozoa, Nematoda and Enchytraeid worms. This can result in higher numbers of mesofauna in mor forest soils than in mull soils and an inverse correlation of mesofauna populations with decomposition rates in different biomes (Swift *et al.*, 1979). Table I shows higher levels of microfauna in mor soils as well.

Less acidic vegetation, or base-rich soils allow the macrofauna to become established and rapidly break down the litter and mix it with the underlying mineral soil. Edwards and Heath (1963) reported that earthworms in mull soils were responsible for more than doubling leaf disappearance rates from the soil surface. The importance of macrofauna in the comminution of bulky food resources (litter) is a function of animal size, structure of its mouth-parts and the physical nature of the food resource. For example, the way in which an earthworm tears large leaf fragments restricts the worm to feeding on soft plant materials. Thus we can expect marked changes in faunal populations when converting a deciduous forest to a conifer forest or vice versa, especially if the conversion causes a change between mull and mor conditions.

Zlotin and Khodashova (1980) contrasted first-year decomposition rates for leaf litter of several deciduous species in the presence of various soil organisms. Of the total weight loss, which was 33%–59% of the original leaf litter weight, the larger soil fauna (meso plus macro) consistently caused the largest weight loss (Table II). Abiotic decomposition (due to solar radiation, temperature, precipitation, etc.) and soil microflora were responsible for the least weight loss. Although some of the weight loss was no doubt due to the comminution and loss of small particles through the mesh bags, the reduction in particle size would speed the decomposition of those particles and the rate of loss by leaching. The activities of the larger fauna create a

Table II. Influence of abiotic factors and various groups of organisms in the first-year decomposition of leaf litterfall.[a]

	Tree species		
	Oak	Aspen	Elm
Starting leaf wt. (g)	10.0	10.0	10.0
First-year wt. loss (g)	3.4	4.3	5.9
Due to:			
Abiotic decomposition	0.6 (17%)	0.6 (14%)	0.5 (8%)
Biotic decomposition			
Microorganisms	0.5 (15%)	0.2 (5%)	0.4 (7%)
Microfauna	1.0 (29%)	0.9 (21%)	2.2 (37%)
Meso, Macrofauna	1.3 (39%)	2.6 (60%)	2.8 (48%)

[a] From Zlotin and Khodashova (1980).

wide spectrum of secondary resources and faeces which may then be decomposed by a diverse community of microfauna, bacteria and fungi. This suggests that microfauna, bacteria and fungi influence decomposition more than macrofuna in the later stages of detritus decomposition.

The feeding activities of soil fauna may directly influence rates and patterns of nutrient availability. For example, in decaying wood the entry of wood-boring animals caused a rapid release of nutrients previously immobilized in fungal mycelium (Ausmus *et al.*, 1976). Syers *et al.* (1979) demonstrated that earthworm activity increased the mineralization of organic N and nitrification; much of the organic nitrogen is "passed through" the organism, the resulting casts have lower C/N ratios and increased microfloral decomposition and mineralization. The production of casts, faecal material, nest building activities, etc. may also create accumulation points where mineralization rates may be higher than in other areas of the soil (Krivolutskii and Pokarzhevskii, 1977).

There also are examples of increased litter decomposition and nutrient cycling in mor soils by discing (Gosz, 1981). These indicate man's actions as a macrofaunal agent (litter fragmentation and soil disturbance) have important management value. This is an important research area.

B. Role of Soil Microflora

I will divide soil microflora into fungi and bacteria to simplify their discussion and concentrate on a number of contrasting properties. The mycelial growth of fungi is of major signigcance in decomposition because it enables penetration and invasion of detrital materials (Griffin, 1972). The hyphae may also be aggregated into strands or rhizomorphs to aid penetration, which is followed by the production of a frond-like mycelium that can exploit planes of weakness between cells and within the molecular lattice of structural polymers within cell walls.

An important aspect of the mycelial growth form is the ability to transport or translocate nutrients so that resources which are limiting in one microsite can be supplied from elsewhere. This translocation normally spans a distance of several microns but basidiomycetes which form rhizomorphs may translocate materials over several meters (Swift *et al.*, 1979).

In contrast, the unicellular microbes are more adapted to surface habitats. These are rapidly exploited because the very small size of the bacterial cell allows colonization of crevices and pores. Thus, bacteria are adapted to the occupation of particulate detritus where the surface to volume ratio is high

(Parr *et al.*, 1967). The size of colonies formed at a site may be small, but dispersal is rapid through the water films and porous systems of detritus. Many of the species are opportunistic, often dormant, but capable of rapid growth to exploit additions of readily metabolized resources. Freshly fallen litter has a rapid initial increase in microbial populations which then dies away as the metabolism of simple sugars, pectins and amino acids is completed. The remaining materials (mainly cellulose and lignin) which comprise most of the tissue weight, are decomposed more slowly by other micro-organisms (Winogradsky, 1924; Garrett, 1963).

The fungal microflora also has groups which are primary colonizers of plant tissue and are dependent on simple non-polymeric substrates (sugar fungi). As the simple organic compounds are exploited, these fungi sporulate and disperse, the mycelium dies off, and the fungi remain dormant until similar resources become available again. This may occur again in the same detritus material after the celluloytic group of fungi provide sugars by the hydrolysis of cellulose (e.g. Basidiomycetes).

As with soil fauna, there are differences in numbers of microflora in different areas. Swift *et al.* (1979) report a general increase in bacterial cell counts and hyphal lengths in the soil with decreasing latitude (Table I). It is also likely that the turnover time of microbial populations is far shorter at low latitudes (higher temperatures) resulting in less microbial immobilization of potentially limiting nutrients at these latitudes. At intermediate latitudes microflora activities are also markedly influenced by variations in detritus quality. The formation of mull and mor humus in European woodlands under the same climatic conditions, and even under the same forest vegetation, provides an example: decomposition rates in deep, organic mor soils (pH 3.5–5.0) may be inhibited by the tanning of cellulose by protein-phenol complexes (Gosz, 1981; Handley, 1954). The acidic litter produced on these sites tends to inhibit bacteria and promote fungal growth whose metabolites further decrease pH. Less acidic vegetation, or base-rich soils which neutralize the organic acids, allow the development of mull soils (pH 5.0–7.0) which favour bacteria.

The release of nutrients by microflora during decomposition (mineralization) has been studied frequently. Generally, the net mineralization of an element relates to its availability to the decomposer organism. Thus, C (or energy) is usually plentiful in the early stages of decomposition, but elements such as N and P may be deficient. Net immobilization of an element will prevail until the element is accumulated in quantities which do not limit decomposer growth, and then net mineralization may occur. Immobilization and mineralization processes during decomposition will be addressed in other sections of this chapter.

III. INFLUENCE OF TREE VEGETATION

A. Immobilization in Biomass

The uptake and use of nutrients by vegetation may be a major factor influencing the supply of available nutrients later in the life of a stand. The peak nutrient requirement occurs during the period of canopy development. Once it has closed and foliage quantity has become relatively constant, nutrient demands are reduced because tree growth consists mainly of the accumulation of wood with low nutrient concentrations (see Chapter 3). When heartwood formation begins, this type of wood makes up most of the increase in dry weight. Rodin and Bazilevich (1967) list the order of nutrients immobilized in tree increment as:

$$\begin{array}{ccccccccc} & & & & & & \mathrm{P} & & \\ \mathrm{N} & > & \mathrm{K} & > & \mathrm{Ca} & > & \mathrm{Mg} & > & \mathrm{Fe} \\ & & & & & & \mathrm{S} & & \mathrm{Mn} \\ & & & & & & \mathrm{Al} & & \mathrm{Na} \\ & & & & & & \mathrm{Si} & & \end{array}$$

In general this is true for both conifers and deciduous species, however, there are exceptions (e.g. *Populus tremuloides* (aspen)) where Ca is immobilized most.

As nutrient demands decrease because of the dominance of wood in the annual increment, the order of element immobilization may change. For example, the immobilization of N and P may decrease more than Ca or Mg because of much lower N and P concentrations in wood compared to Ca and Mg. The development of heartwood enhances this pattern (see Chapter 7).

There is little information on below-ground nutrient accumulation in root biomass (see Chapter 6). Many studies have assumed that decreasing above-ground productivity and biomass accumulation are accompanied by decreases in these factors for roots as well. However, decreased above-ground productivity with increasing stand age may indicate largely a shift in the balance between above- and below-ground components Grier *et al.* (1981). In a young stand of *Abies amabilis* (Pacific silver fir), 55% of the total net productivity was invested annually in the production of fine roots and mycorrhizas while in a mature stand this was 69%. These findings suggest that in mature stands, proportionately more dry matter is allocated to below-ground structures to increase the ability to obtain nutrients and water. Thus, the apparent decline in total productivity with stand age may not be as great as previously thought. (The nutrient content of root litter and its role in nutrient cycling is discussed in Chapter 6.) However, it remains plausible to hypothesize that with increasing stand age, productivity, biomass accumulation and nutrient accumulation will decline.

Although the additional immobilization of some nutrients in tree biomass may become negligible in older stands, nutrient availability to the tree may continue to decrease because of other immobilization processes. For example, increased nutrient accumulation occurs in the forest floor with stand maturity (Foster and Morrison, 1976; Turner, 1975). The nutrient content of litter may equal nutrient uptake (i.e. no accumulation in living biomass) but the relatively low decomposition rates in some stands may not mineralize nutrients in the forest floor at a rate equal to litterfall nutrient additions. This is typical of conifer and deciduous forests which develop mor humus layers. Nutrients and detritus then accumulate on the forest floor and nutrient uptake must occur from the mineral soil layer or must decrease to match the decreased nutrient availability (Gosz, 1981).

In a mixed forest, species changes during succession can result in variations in nutrient immobilization in biomass. Where each seral stage is dominated by different species, productivity is likely to rise and fall with the establishment and decline of the various species (Egunjobi, 1969; Golley, 1965). Thus, the wave-like pattern of productivity and biomass accumulation may result in a concurrent pattern of nutrient immobilization in the biomass. In a succession with many species, the replacement may occur more rapidly and smoothly without large variations in accumulated biomass. The immobilization of nutrients would be expected to increase in a similar fashion. Some successions consist of marked changes in the nature of the species, such as from deciduous to coniferous. In addition to increased nutrient immobilization in biomass, the nature and nutrient content of litterfall may change markedly, influencing decomposition and nutrient immobilization in detritus (see Section VI).

Species differ in their ability to extract base elements from the soil. Leaf tissue and litter of conifers as a group contain lower base element concentrations than those of hardwoods; however, certain conifer species e.g. *Picea abies* (Norway spruce) and *Thuja occidentalis* (northern white cedar) contain more Ca (1.96% and 2.16%, respectively) than a number of hardwood species, such as *Quercus alba* (white oak) (1.36%) and *Fagus grandifolia* (American beech) (0.99%) (Lutz and Chandeler, 1946). Spurr and Barnes (1973) reported that *Juniperus virginiana* (eastern red cedar) had a much greater capacity to remove base elements from the soil than an adjacent *Juniperus communis* (common juniper). Litter with higher base content is less acid, less able to complex proteins and much easier to decompose (Swift *et al.*, 1979; Gosz, 1981). Mixing these high base materials with other litter increases the decomposition of the other litter as well. This also presents some exciting management possibilities for increasing the available nutrients in a stand by using mixtures of species or a succession of species. European experience indicates that mixing hardwoods in with conifer stands of pine and spruce can increase decomposition rates, reduce acidity and stimulate nitrification (i.e. increase nutrient availability). The beneficial effects of hardwood mixtures in spruce stands in Sweden appear to persist even after the hardwoods have disappeared (Lutz and Chandler, 1946).

B. Litter Quantity and Quality

During the life of a stand, nutrient availability and uptake varies along with total litterfall and the nutrient content of litter reflects this (Fig. 1). Nutrient pools change rapidly when a stand is first established, and numerous reports refer to a phase of declining tree growth during middle age associated with a progressive development of nutrient deficiency (Williams, 1972). The development of this deficiency is paralleled by an accumulation of nutrients in litter layers (see Gosz, 1981). Variation of nutrient content of litter is a result of variations in both the quantity of litter produced and its nutrient content (Rodin and Bazilevich, 1967). We can expect patterns of total litterfall to parallel productivity patterns (Rodin and Bazilevich, 1967). The nutrient content of litterfall is related to nutrient availability, uptake and retranslocation to young tissues (Chapters 3 and 7). With stand maturity the nutrient

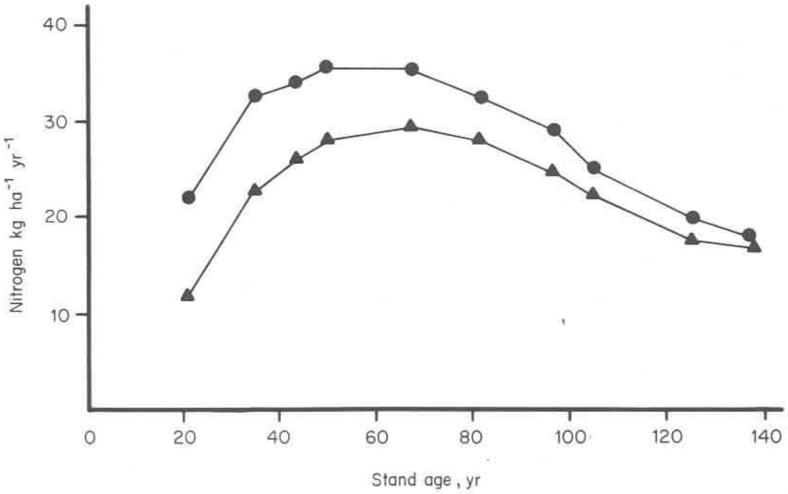

Fig. 1. Changes in N cycling for *Picea abies* in Russian stands 22–138 years-old. ●–●, uptake into tree; ▲–▲, return in litter (from Cole and Rapp, 1980).

concentrations in litter decrease because of reduced uptake as well as increasing proportions of woody litter which has lower nutrient levels. There are relatively large inter- and intra-species differences in both the uptake of nutrients and nutrient content of litter. Gosz (1981) reported ranges of N concentrations in litter of 0.4–1.3% and 0.5–1.8% for different conifer and deciduous forests, respectively. A species growing on a site with high nutrient availability will have higher nutrient concentrations in its litter: Lamb and Florence (1975) reported 0.5% N and 0.035% P in *Pinus radiata* (radiata pine) litterfall on a sand podzol site while a better terra rossa site had litterfall with 0.8% N and 0.10% P. Manipulating the nutrient availability, such as with fertilizing, also causes these changes: Miller *et al.* (1976) reported the N% of litterfall increased from 0.4% to 1.0% during a 6-year period of fertilization with 504 kg N $ha^{-1} yr^{-1}$.

(1) Woody litter

After canopy closure, net increment is primarily in woody tissue and the litterfall of natural stands after canopy closure demonstrates increasing proportions of woody types of litter, leading to lower nutrient content of litterfall especially in natural, older stands. In plantations or managed stands, the increase in woody litter may not be as marked because of commercial thinning which removes the larger stems before natural mortality occurs. The majority of natural woody litter in these stands would be smaller branches. The woody slash (tree tops) added to the forest floor during harvesting would have higher nutrient concentrations and cause a higher nutrient transfer to the forest floor. Will (1968a) estimated that slash from a first thinning waste in a *Pinus radiata* plantation would contain 260 kg N ha^{-1} while litterfall contained only 31 kg $ha^{-1} yr^{-1}$.

(2) Root litter

Root litter information is badly needed for all forest species. In view of the large fine-root production and rapid turnover rates recently reported (see Chapter 6) root litter may be greater than overstory litterfall for many forests. Data for the nutrient content of root litter, changes with age, and species differences are scarce. Miller *et al.* (1979) reported increased N levels in root litter on fertilized plots, and Staaf and Berg (1977) reported the N content of below-ground litter as over twice the N content of above-ground litterfall. Aber *et al.* (1982) reported fine-root litter is only a temporary sink for N (<6 months) as it rapidly decays and its N content is mineralized. There was no evidence of translocation of N out of roots during the mortality period as the fine-root litter had N concentrations similar to living fine roots.

Swift *et al.* (1979) gave data for eight conifer species showing root wood may decay much faster (up to 3 times) than stem wood with large differences among species.

(3) Litterfall timing

There is an important interaction between the categories of plant litter and the timing of their addition to the forest floor. The dominant litterfall period for northern hemisphere forests is the autumn, primarily because of leaf and needle fall. However, other categories may be added at other times: Gosz *et al.* (1972) demonstrated that additions of nutrient-rich aborted fruits and insect frass occurred during the summer months, which could markedly stimulate decomposition rates. The input of pollen and bud scales occurs in late spring. Although relatively small in magnitude, the high nutrient levels in these materials cause not only their rapid breakdown but an increased breakdown of other materials (Zlotin and Khodashova, 1980). This "manuring effect" may be an important aspect of the decomposition process in forests, however, it has not been well studied.

Inputs during the winter and early spring are primarily woody (branches, stems) although winter storm activity may cause green needles and living branch material to be removed. The influence of this type of winter litterfall on the overall decomposition process has not been quantified.

(4) Chemical and physical quality

The quality of the different forms of litter varies markedly and affects rates of immobilization, decomposition and mineralization. The major plant organs have characteristically different rates of decomposition (Table III). Reproductive tissues decompose faster than leaves, which decompose faster than

Table III. Decomposition constants for major types of tree tissues of forests of different climates.[a]

	Decomposition constant k (yr^{-1})	
Tissue	Temperate deciduous forest	Tropical rain forest
Reproductive	2.22	9.65
Leaf	1.61	2.55
Wood[b]	0.33	0.37

[a] From Swift *et al.* (1979).

[b] Wood includes branches (> 2 cm dia.) and twigs (< 2 cm dia.).

wood, and these differences hold whatever the climatic conditions or rate at which decomposition proceeds (Swift *et al.*, 1979). These categories of litter could be subdivided further to distinguish different forms of reproductive tissues, different size classes, different age classes or different species. Groupings of this type have group-specific decomposition rates. The groups differ both physically and chemically. The toughness of litter material may influence the palatability to animals (e.g. hardwoods *vs* conifers) while certain chemicals (e.g. polyphenols) may inhibit both animal and microflora activity. The decomposition rates of these substrates are dependent on proportions of easily used *vs* recalcitrant substrates and their concentrations of essential elements.

The carbon components of litter (e.g. sugars, proteins, hemicellulose, cellulose, lignin, waxes, phenols) differ markedly in their rates of decomposition, with sugars decomposing most rapidly and phenols least rapidly (Minderman, 1968; Mikola, 1955). A decomposition rate estimate from a summation of the decomposition rates of individual organic components overestimates actual decomposition (Swift *et al.*, 1979), probably because of microbial resynthesis of secondary metabolites which break down at a slower rate (Clark and Paul, 1970). There commonly is an increase in N concentration during decomposition which represents a movement of organisms into the material as well as from precipitation, leaf wash and N-fixation.

There are significant inverse correlations between initial lignin percentage and decomposition rate (Fogel and Cromack, 1977). Initial concentrations of essential inorganic elements in litter have also been correlated with decomposition rates, especially nitrogen (Merrill and Cowling, 1966; Gosz *et al.*, 1973). Since lignin is a difficult organic compound to decompose and since N is, in many ecosystem processes, a limiting element, it is reasonable that the lignin : N ratio of fresh litter would be an even better predictor of decomposition rate than either alone (Melillo *et al.*, 1982).

It is clear that the choice of species for a plantation is a prime factor in the nutrient availability in the plantation. Conifer species generally have lower litter N (0.3–1.3%), cause greater forest floor accumulations (10–70 t ha^{-1}), lower decomposition (0.008–0.69 k yr^{-1}) and mineralization (50–100 kg ha^{-1} yr^{-1}) rates and higher nutrient immobilization than deciduous hardwood species (Gosz, 1981; Rodin and Bazilevich, 1967; Aber and Melillo, 1982; Swift *et al.*, 1979). There is enough variation among the species of each group to cause considerable overlap for most of these factors, however.

There may also be *considerable* chemical variation among individuals and ecotypes within a species which could affect decomposition. Lignin percentage has been demonstrated to vary with moisture, temperature, nutrient stress (Gosz, 1981; Loveless, 1962) and tissue age (Swift *et al.*, 1979).

Production of polyphenols also is markedly affected by alteration of external environmental factors, including nutrient availability. Davies *et al.* (1964a) reported anthocyanidin levels in N- and P-deficient *Pinus sylvestris* needles up to three times higher than those of control plants. They also found higher leaf anthocyanidin levels both between and within species on mor sites compared with mull sites. Increased production of these polyphenols under stress conditions decreases litter decomposition rates by complexing with plant protein, cellulose and hemicellulose, by coating decomposable compounds with resistant polyphenol complexes, and reacting with microbial enzymes (Benoit *et al.*, 1968). Polyphenolic compounds of plant origin are highly implicated as modifiers of the decomposition, immobilization and mineralization processes, and there is sufficient evidence to suggest differences in the polyphenols, and concentrations may explain many observed differences in effects (Swift *et al.*, 1979). There is a need for additional research on this important area, however.

Organic acid production in plants may also increase in response to environmental stress, and the increased acidity may be a major factor in the production of resistant protein-phenol complexes (Davies *et al.*, 1946b). Less acid conditions, such as those on mull sites and base-rich soils (pH 5–7), may lead to less stable complexes and more *rapid* mineralization of the proteins in litter, leading then to greater N availability and plant uptake, and a reduction in phenol production (Davies *et al.*, 1964a).

(5) Influence on immobilization and mineralization

Melillo *et al.* (1982) demonstrated that decomposition during the first year can also be described by a inverse linear relationship between the percentage of original weight remaining and the N concentration in residual material (Fig. 2). This increase in N concentration (net immobilization) continues until the N concentration is high enough to satisfy the requirements of the decomposer population and is referred to as the critical N percentage (Berg and Staaf, 1981). After this point the percentage of original weight would continue to decrease while the N concentration would stay about the same (a vertical line in Fig. 2). In a hardwood forest in northeastern US, N was immobilized in yellow birch leaf litter for the first 8 months during which the C : N dropped from 62 : 1 to below 30 : 1 (Gosz *et al.*, 1973). The absolute N content of the leaves then dropped, paralleling weight loss suggesting net mineralization, but some of the net loss may also have been due to export by animals, translocation in fungal hyphae, or loss in fungal spores (Dowding, 1976). Lutz and Chandler (1946) suggested that the release of N from litter takes place at a critical N percentage of between 1.7% and 2.5%. This corresponds to a range of C : N ratios of 30 : 1 to 20 : 1, respectively. Berg and

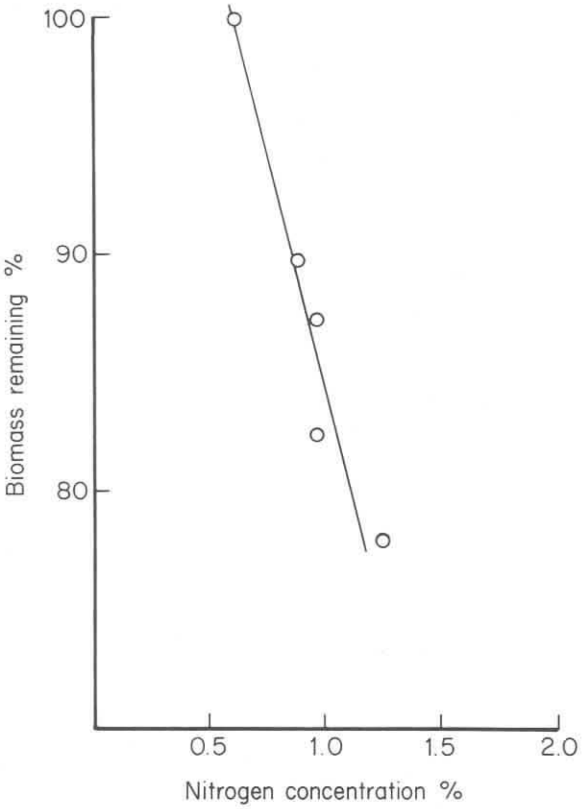

Fig. 2. Relationship between weight loss and N concentration in the remaining material for decomposing *Acer saccharum* leaves in a northern hardwood forest, New Hampshire, US (from Melillo *et al.*, 1982).

Staaf (1981) demonstrated that the critical N percentage varies widely, however. *P. sylvestris* cones appeared to release N at 0.3% and needles released N at 0.6%. The critical N% appears to be correlated with decomposition rate: high critical N percentage in tissue having high first-year total weight loss, this supports the discussion that organic chemical composition and environment also influence N mineralization.

The relationship between immobilization and mineralization is crucial in nutrient availability in forest systems. Aber and Melillo (1980) presented an interesting set of relationships for six leaf litter types designed to predict the amount of N immobilized per gram original weight, per gram of weight loss, and the percent of original weight remaining when the switch from net

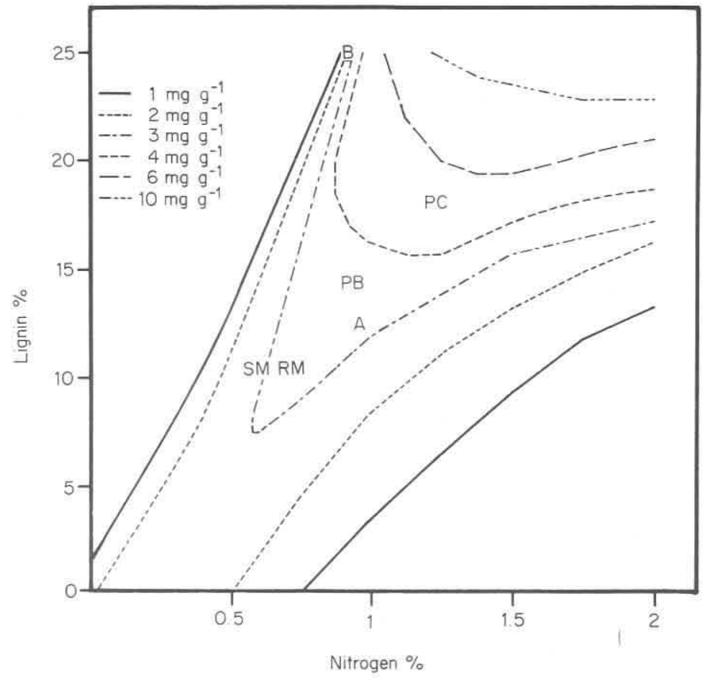

Fig. 3. Total N immobilized in leaf litter during the first year of decomposition in a northern hardwood forest, US, as a function of initial lignin and N concentrations of the leaves. The lines show the total milligrams of N immobilized per gram of original leaf litter for the 1-year period. The letters identify the six species of leaf litter used in deriving the lines, plotted according to their initial lignin and N concentrations: PC–pin cherry; PB–paper birch; A–white ash; RM–red maple; SM–sugar maple; B–American beech (from Aber and Melillo, 1982).

immobilization to net mineralization occurs. Figure 3 shows net N immobilized in the first year of decomposition in relation to initial lignin and N percentages of the six species. The highest immobilization rates (g N immobilized g^{-1} litter input yr^{-1}) occurred in litters high in lignin or in N. This is because total immobilization increases with lignin content while rate of decay increases with N content. Recall that high decay rates are correlated with high critical N percentage. Aber and Melillo (1980) suggest the immobilization by high lignin species would be primarily as protein-lignin or protein-polyphenol complexes while high N species would have the N immobilized in microbial biomass or other by-products. Berg and Staaf (1981) found a significant linear relation between the total increase of N in decomposing litter and the increase of N in the lignin fraction ($r = .898$, $p < .001$). Swift *et al.* (1979) summarized data confirming that lignin products, modified by microbial action, may be major contributors to humus formation which holds protein-N in an immobilized form.

Gosz (1981) proposed a general model of the interactions of several processes on N availability in low and high nitrogen sites (Fig. 4). Vitousek *et al.* (1982) demonstrated a significant positive relationship between the N content of litterfall and N mineralization rates in seventeen forests in the US. These studies suggest a range of N values for the low to high N availability models of Figure 4: N in litterfall, 5–100 kg $ha^{-1} yr^{-1}$; litter C/N ratio, 180 : 1–20 : 1. Increasing N availability can increase the movement of N through the system by increasing N in litterfall (higher N percentage in senescent tissues), decreasing polyphenol and organic acid levels, and increasing decomposition and mineralization rates which enhance the higher N availability. Increasing the quantity of N (fertilization) has increased N availability (Miller *et al.*, 1979) as do practices which simply increase the movement or cycling rate by increasing litter decomposition. Liming (raising pH) and discing have been found effective in increasing N availability (Williams, 1972) as well as fire (Gosz, unpublished data). A great deal of silvicultural research is possible in this area.

C. Throughfall

Nutrients, carbohydrates (energy), or organic compounds in throughfall or leaf wash may affect nutrient availability in litter. Nutrients and carbohydrates may increase nutrient availability while organics such as phenols may decrease it in the same way the polyphenols in litter complex and reduce the availability of nutrients in that material.

Decomposition of detritus often shows seasonal patterns. Rapid growth of mycelium after leaf fall is the result of carbohydrates and nutrients in leaf fall and of leaf wash during the preceeding senescent phase (de Boois and Jansen, 1976). Sugars disappear rapidly from fallen leaves, and carbohydrate availability can become a limiting factor to microbial growth in the litter layer. Minderman (1968) showed the fermentation of fallen leaves is a rapid process during the first 6 months after leaf fall, the rate of fermentation being dependent upon the forest floor studied. Some of the increase in microbial activity found following precipitation during the summer months is correlated with increased carbohydrate and element concentrations in throughfall (de Boois and Jansen, 1976).

While the nutrient content of throughfall (see Chapter 3) is less than that of litterfall, its immediate availability plays an important role in the dynamics of various ecosystem processes. In some forests the nutrient

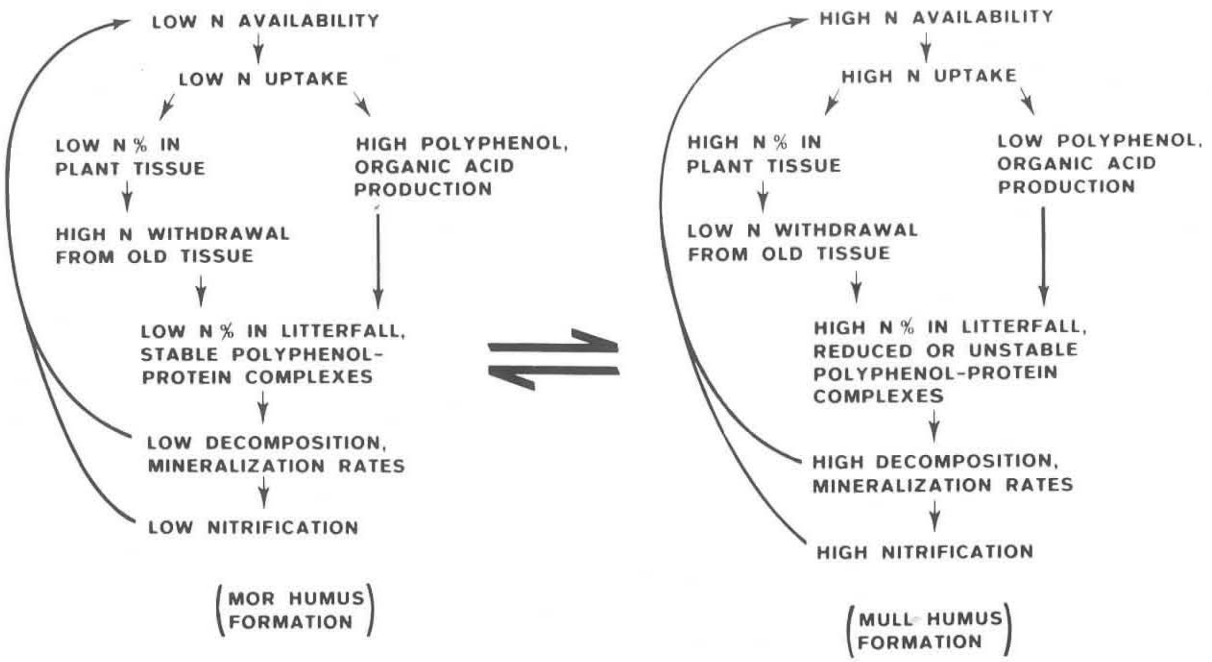
LOW N AVAILABILITY
LOW N UPTAKE
LOW N% IN PLANT TISSUE
HIGH POLYPHENOL, ORGANIC ACID PRODUCTION
HIGH N WITHDRAWAL FROM OLD TISSUE
LOW N% IN LITTERFALL, STABLE POLYPHENOL-PROTEIN COMPLEXES
LOW DECOMPOSITION, MINERALIZATION RATES
LOW NITRIFICATION
(MOR HUMUS FORMATION)
HIGH N AVAILABILITY
HIGH N UPTAKE
HIGH N% IN PLANT TISSUE
LOW POLYPHENOL, ORGANIC ACID PRODUCTION
LOW N WITHDRAWAL FROM OLD TISSUE
HIGH N% IN LITTERFALL, REDUCED OR UNSTABLE POLYPHENOL-PROTEIN COMPLEXES
HIGH DECOMPOSITION, MINERALIZATION RATES
HIGH NITRIFICATION
(MULL HUMUS FORMATION)

Fig. 4. Influence of the interactions of several processes on N availability in low and high N sites. Increasing or decreasing the N availability may cause a marked change in plant litter and the interaction of processes (from Gosz, 1981).

content of throughfall is one-half that of litter fall (Rolfe *et al.*, 1978); however, even where it is substantially less, its importance in stimulating decomposition processes may be high. The higher rate of respiration in the F layer of the forest floor even after the supply of dissolved nutrients had decreased may indicate that an added supply of nutrients has a priming effect on the decomposition of older leaf matter.

Various toxins or phenols in throughfall could influence many types of organisms in adverse ways. Laboratory experiments show that leaf extracts influence many microbial processes, and it is reasonable to assume these leaf extracts would be present in throughfall. The water extractable organics in leaf litter affect soil fauna (decreased palatability, Heath and Arnold, 1966) and flora activities (decreased respiration). Water soluble organics also decrease N mineralization and nitrification (Rice, 1974; Lodhi and Killingbeck, 1980). Thus, potential stimulators and inhibitors may occur in the same solution. Little is known of the total or net effect of this throughfall or whether certain groups of organisms are influenced more under one forest species than another. Studies of this process in the field are certainly warranted.

Another aspect receiving little study is the spatial redistribution of moisture by the canopy and its change in chemical composition. Ford and Deans (1978) demonstrated predictable patterns of throughfall caused by the regular spacing in a spruce plantation. The pattern of water flux was correlated with the distribution of fine roots, greater throughfall and root concentration near tree stems (see Chapter 2). Not all forests can be expected to have the same pattern because of differences in leaf morphology, branching pattern and planting density or spacing. We can expect spatial patterns of decomposition, mineralization and water availability which the trees are reacting to. Most spacing studies have dealt with growth, pruning or tree form. It would seem important to understand how spacing affects factors influencing nutrient availability and root dynamics.

IV. INFLUENCE OF UNDERSTORY VEGETATION

The shrub and herb layer components of forest stands are often overlooked. Although dense understory growth may use moisture and nutrients at the expense of forest trees, they may also be important influences on nutrient cycling within forest stands.

Understory productivity can range from essentially zero to 1730 kg ha^{-1} yr^{-1} (Gosz, 1980). Low values are commonly found in conifer stands, but even here they may account for considerable biomass. Maclean and Wein

(1977) found the understory biomass in *Pinus banksiana* (jack pine) ranged from 1–6% of the ecosystem biomass in old stands (57 years) to 88% in young stands (16 years). These authors pointed out that understory species often accumulate certain elements and may have an even greater impact on nutrient immobilization and cycling than their biomass indicates. They found the understory in 13–16-year *P. banksiana* stands to have 25% of the N and Ca, 30% of the P, 40% of the Mg, and more than 65% of the K in the above ground ecosystem. Gosz (unpublished) found the productive herbaceous layer of a natural aspen forest accumulated 60 kg K $ha^{-1} yr^{-1}$ and 47 kg N $ha^{-1} yr^{-1}$, amounts greater than the annual uptake by the tree component.

Understory growth and litter production is related to the light penetration through the overstory (Bray and Gorham, 1964). Thus, understory litterfall generally is inversely related to overstory litterfall for a given forest type and is often some 3–28% of total litterfall. There can be large differences between different types of forests. Angiosperm forests commonly have higher understory litterfall than conifer forests. One of the highest understory litterfalls measured, 1317 kg $ha^{-1} yr^{-1}$ in an old aspen forest in New Mexico, USA was 31% of the total litterfall (which included stem fall) and 75% of the overstory leaf litterfall (Gosz, 1980).

The higher nutrient concentrations in understory litter increase markedly the percentage contribution by the understory to the total nutrients in litterfall. Tappeiner and Alm (1975) reported that in *Pinus resinosa* (red pine) stands there was significantly more N, Ca and Mn, under the shrub *Corylus cornuta* (hazel) and under herbs there was more than twice the amount of K in the litterfall than where these undergrowth layers were absent. In *Betula papyrifera* (paper birch) stands such differences beneath these undergrowth layers were not great, and they had less effect on the nutrient cycle. Turnover rates of nutrients in the forest floor were different under each type of undergrowth, and in *P. resinosa* stands, the forest floor under hazel and herbs appeared to decompose more rapidly than under pure pine, but not as rapidly as under either hazel or herbs in the birch stands.

In the *P. resinosa* and *B. papyrifera* stands above, Comerford and White (1977) found that the shrub understory modified throughfall within the forest ecosystem considerably. The pine stand plus shrub layer had a leaching increase of 11% for N to 98% for Ca. In the birch stand increases were 80% for N to 194% for Ca. These differences must contribute to the faster decomposition and turnover rates for the forest floor in stands with a significant understory component. However, concentrations of some nutrients in throughfall decrease as they pass through the understory foliage layer (Brown, 1974). Most results suggest that managing the understory as well as the overstory may allow the development of more rapid nutrient cycling, higher nutrient uptake and perhaps increased productivity of the overstory. This remains to be tested.

V. INFLUENCE OF HERBIVORES

In spite of a large diversity of herbivorous animals (insects to mammals) their quantitative role in the nutrient cycle is normally thought of as small and omitted from tables and diagrams. However, in some situations their impact may be considerable. Although herbivore consumption in temperate forests is normally less than 10% of the foliage biomass (Bray and Gorham, 1964), they consume living tissue which may have high levels of nutrients and low levels of organic compounds compared with that of litter. A high proportion of the consumed material is passed on to the forest floor in excreta (Gosz *et al.*, 1972). In addition to higher nutrient concentrations, the excreta may have higher levels of water soluble matereials which allow a more vigorous development of a variety of decomposer micro-organisms. Thus, not only the herbivore excreta may be decomposed rapidly but other forest floor material may have an increased decomposition rate as well. Part of this stimulation in decomposition and mineralization may be due to the increased light which reaches the forest floor and increased moisture available to the decomposers (Zlotin and Khodashova, 1980).

The selective feeding behaviour of herbivores may influence the overall decomposition process markedly. Gosz *et al.* (1972) reported that insect hervivores in a northern hardwood forest in the US preferred *Fagus* (beech) leaves to those of *Acer saccharum* (sugar maple) and *Betula alleghaniensis* (yellow birch). Of the three species, normal beech leaf litter is most resistant to decomposition, thus, insect herbivores may markedly influence the contribution of beech to the nutrient dynamics of this forest.

The greater rates of mineralization under the influence of herbivores infer possibly greater plant productivity. Moderate to severe defoliations can increase normal N, P and K contributions in the litterfall by 20 to 200% (Mattson and Addy, 1975). Although studies generally address the negative aspects of herbivory, there are a number of reports of insignificant effects or of an enhancement of productivity, possibly due to this increased nutrient availability. Zlotin and Khodashova (1980) reported that increment losses of oak were insignificant until defoliation exceeds limits of 75% of the photosynthetic biomass. Secondary growth following consumption can often replace consumed foliage rapidly, resulting in a similar or even higher foliage surface area. Successive defoliations of this magnitude, however, would most likely reduce increment.

The role of herbivory warrants much more attention in management practice. Insect grazers may function much like cybernetic regulators of primary production in natural ecosystems. If insect-plant relations are mutualistic in the long term, despite any temporary decrease, serious modifications must be made in the management of grazers in many forest ecosystems (Mattson and Addy, 1975). The possibility of increasing forest productivity by allowing a controlled degree of insect herbivory on the trees is a far cry from many current views of these insect *pests*! The same may be true for root feeding insects.

VI. SUCCESSIONAL CHANGE

Forest plantations may have very different species from those of the previous vegetation type, which may influence many physical and chemical soil characteristics. For example, conifer ecosystems as a group have litterfall which is low in nutrients and high in organic acids. This litter is difficult to decompose and accumulates on the forest floor. Conifer plantations on the same site as natural hardwood forests show a manifest redistribution of nutrients from the soil to the forest floor under conifers (Lamb, 1976; Turner and Kelly, 1977). This removal of the soil nutrients and immobilization in difficult to decompose detritus is a current area of concern.

Where succession results in deciduous hardwoods replacing conifers, there may be a reduction in the forest floor mass, greater decomposition, mineralization and increased nutrient availability (Gosz, 1981). In the Piedmont region of the US, the succession from *Pinus taeda* (loblolly pine) 70 years of age to unevenaged oak was associated with a decrease in the A_0 forest floor layer from 7.1 to 4.8 cm (Alderfer and Merkle, 1941). In northern Minnesota, US, succession resulted in forest floor weights of 37.3 t ha^{-1} (*Pinus banksiana*), 42.0 t ha^{-1} (*P. resinosa*), 77.6 t ha^{-1} (*P. monticola*), and 70.0 t ha^{-1} (*Acer saccharum—Tilia americana*). The decrease in forest floor weight from *P. monticola* to mixed deciduous species was attributed to more rapid decomposition under hardwoods (Alway *et al.*, 1933).

An important aspect of successional change is the possibility that a different species can break down organic matter that was relatively resistant to decomposition previously. Fisher and Stone (1969) suggested the rhizosphere of some conifer species caused the mineralization or extraction of some fraction of soil nitrogen that was resistant to microbial activity before. Will (1968b) reported that the mycorrhizal-root system of *P. radiata* reduced soil organic matter (soil bleaching) to a greater degree than other pines and *Pseudotsuga menziesii*. The magnitude of the root zone influence presumably varies according to species, pioneer species (e.g. larches and pines) having the greatest ability (Tamm, 1975; Stone and Will, 1965). Mycorrhiza-forming fungi apparently utilize very little of the nitrogen bound in humus (Lundeberg, 1970; see Aber *et al.*, 1982 for exception) suggesting that other rhizosphere micro-organisms may be primarily responsible for this N mineralization. This data suggests that the ability of a species to invade a new area may be enhanced by unique plant-micro-organism associations in the rhizosphere acting on certain kinds of organic compounds. More research is needed in this area, and if these results are confirmed, there are some exciting management possibilities in mixed plantings. This may be part of the reason for the greater nutrient availability in pine stands with certain understory species cited earlier.

VII. INTERACTION WITH CLIMATE AND SITE FACTORS

Climatic factors influence decomposition and nutrient availability and, in fact, actual evapotransporation (AET) can be a predictor of decomposition rate (Meentemeyer, 1978). The decomposition rate is often refered to as k, the annual fractional weight loss (Swift *et al.*, 1979). It is commonly estimated by the ratio of litterfall to organic detritus accumulation. These esimates have assumed steady-state conditions and must be used with caution. However, they can be taken as an indication of the magnitude of organic turnover in ecosystems. For broad ecosystem types of different climates Swift *et al.* (1979) found that decomposition constants increase as NPP increases but the range for decomposition values is much larger (Table IV). This results in a general inverse trend between NPP and organic detritus accumulation. Thus, although there may be a litter-composition component to the biome-characteristic decay rates, the obvious conclusion is that environmental factors are a major determinant of the observed differences in the decomposition and litter accumulation values of Table IV.

For a given species or forest type, large differences can also occur in the organic matter accumulation and decomposition rates due to site differences. Florence and Lamb (1974) reported a range of forest floor weights (12–28 t ha^{-1}) for *Pinus radiata* stands of similar age and site quality, but differing primarily in soil type (e.g. terra rossa, sand podzol). Since litterfall was similar, the variation in forest floor weight was attributed to different decomposition rates arising from differences in needle tissue quality, decomposer activity and stand microclimate. Carey *et al.* (1983) reported on 41 first rotation radiata pine stands in New Zealand where forest floor accumulations ranged widely, from 5.9 to 59 t ha^{-1}. The nature and composition of the

Table IV. Production and decomposition in six ecosystem types.[a]

	Tundra	Temperate boreal forest	Deciduous forest	Temperate grassland	Savannah	Tropical forest
Mean NPP ($\mathrm{t\,ha^{-1}\,yr^{-1}}$)	1.5	7.5	11.5	7.5	9.5	30
Meat biomass ($\mathrm{t\,ha^{-1}}$)	10	200	350	18	45	500
Litter input ($\mathrm{t\,ha^{-1}\,hr^{-1}}$)	1.5	7.5	11.5	7.5	9.5	30
Litter accumulation ($\mathrm{t\,ha^{-1}}$)	44	35	15	5	3	5
Decomposition ($\mathrm{k\,yr^{-1}}$)	0.03	0.21	0.77	1.5	3.2	6.0

organic matter varied considerably ranging from a mor-like humus to the lack of a H-layer altogether. These data indicate that for a given species on different sites, a range of litter accumulation may exist which is equal in magnitude to the range found over different climates (Table IV).

Nutrient cycling rates and nutrient availability are expected to parallel patterns of NPP and decomposition constants for different climates. Melillo and Gosz (1982) analysed over 100 data sets from forests of boreal to tropical environments in both northern and southern hemispheres to assess nutrient cycling and nutrient use efficiency. Litterfall was used on the basis that nutrient levels in litter are a function of nutrient availability and efficiency of retranslocation or use. The data of Table IV could be used to predict that the nutrient content of litterfall would be highest in the productive tropical forest and lowest in boreal conifer forests. A plot of the C/N ratio in litterfall *vs* the N content of total litterfall supports this view (Fig. 5). Since the X variable is the denominator of the ratio for the Y variable, a relationship of the form $Y = 1/X$ would be expected if there were *no* functional relationship between nutrient circulation and litterfall mass (i.e. nutrient circulation does not affect organic matter production, and the efficiency of nutrient use does not change with differences in nutrient availability). Vitousek (1982) and Melillo and Gosz (1982) concluded this was not the case. The actual distribution of data differs significantly from the relation $Y = 1/X$. Furthermore, each biome type plots along different portions of the curve, the most productive (i.e. tropics) associated with the highest cycling rates. However, there is overlap among the biomes, and some tropical sites plot with the much less productive conifer sites (Herrera, personal communication). Some conifer plantations on former deciduous sites continue to plot with other deciduous

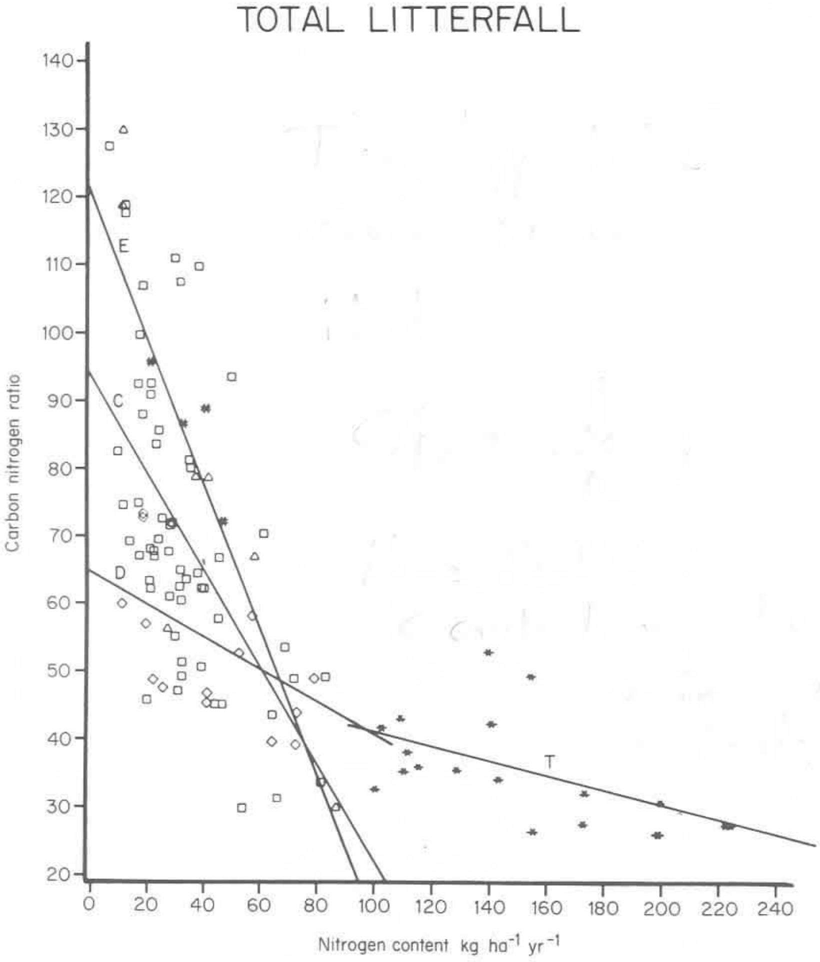

Fig. 5. Relationship of the C/N ratio to total N content of total above ground litterfall in forest ecosystems. Data from 102 forest sites world wide. Forest type: □ = conifers (C), ◇ = deciduous (D), △ = eucalypt (E), * = tropical (T). Lines C, D, E and T indicate the regression line for the various ecosystems (from Melillo and Gosz, 1982).

forest sites (Melillo and Gosz, 1982). In the 41 *P. radiata* stands studied by Carey *et al.* (1983), there was a significant ($p < 0.05$) negative relationship between site index and the N content of the forest floor. They interpreted this to mean the rate of N cycling increases with increasing site index. An increase in site index from 24 to 32 would be associated with a reduction in forest floor N content by 88 kg ha^{-1}, other factors being constant. These differences in N cycling and efficiency of use result from an ability to make use of various nutrient-conserving mechanisms ranging from physiological to mutualistic interactions (Gosz, 1981; Jordan and Herrera, 1981). Regardless of the type of community or site characteristics, the efficiency of use seems related to the availability and cycling of the nutrient (resource availability) which is a promising unifying concept.

VIII. SUMMARY: MANAGING NUTRIENT AVAILABILITY

A primary factor in understanding nutrient availability and cycling rates is that the growth of the forest will cause nutrients to be retained in biomass or litter, thus reducing nutrient availability. This is a normal pattern and most plant species, commonly those used in plantations, have evolved mechanisms to deal with reduced availability. Understanding those mechanisms as well as the nutrient availability necessary for the optimum production potential at that site are fundamental to managing nutrient availability. For example, a species may be able to store and retranslocate most of the nutrient needed for the production possible at that site. Increasing nutrient availability (e.g. by fertilizing) may increase nutrient cycling rates but not increase productivity because other environmental factors may be limiting carbon fixation. Where one or more nutrients are limiting, increasing their availability will no doubt increase cycling rates and carbon fixation. Unfortunately, most of our data on managing nutrient availability comes from "trial and error" fertilizer studies. Managing the biological factors influencing nutrient availability has received much less attention but promises to be a fruitful research area.

The fauna of a site are instrumental in the comminution of forest litter which speeds its decomposition and mineralization of nutrients. They may be responsible for some mineralization themselves. Management techniques, such as discing, simulate and augment the activities of macrofauna. This is a rather expensive management technique and care would need to be exercised to avoid injuring surface roots. Managing soil fauna to accomplish the same activity is an exciting possibility. This would seem best accomplished by managing for the type of litter produced by the plant (i.e. base-rich, low lignin, low polyphenol). Large woody material is normally removed from plantations in commercial thinnings or harvests and therefore the type of litter of concern is principally foliage and branch material. The choice of species is an important factor in the quality of litter, and numerous studies have contrasted decomposition rates for different species. Managing understory species may provide a valuable method of modifying the effect of overstory litter. In addition, a given species may vary the quality of its litter as a result of different environmental conditions, soils and nutrient availability. This may explain much of the overlap among biomes in Fig. 5. The model of Gosz (1981) suggests that increasing the nutrient availability changes the litter quality, causing increased decomposition and maintaining higher nutrient availability (Fig. 4). A practice such as liming may accomplish the same because of its affect on soil and litter pH. Low nutrient availability results in litter which is slow to decompose and this reduces nutrient availability further. Somewhere in between these two situations is a condition where nutrient availability is maintained at a high enough level by biological processes to allow the most economical forest production. Some valuable research would be the identification of combinations of management practices (forest species, understory species, fertilization, discing, liming, fire, etc.) which would create a nutrient availability condition that would maintain itself with minimal additional effort. This also requires research to identify what that additional effort is, and when it should be applied. There alsô must be diagnostic studies performed to identify the plant or process characteristics which will identify the current condition of the stand and rate of change. The above types of research would lead to an innovative and sophisticated management of forest stands.

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